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Modeling sensitivity of grain yield to elevated temperature in the DSSAT crop models for peanut, soybean, dry bean, chickpea, sorghum, and millet

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ABSTRACT

Crop models are increasingly being used as tools to simulate climate change effects or effects of virtual heat-tolerant cultivars; therefore it is important that upper temperature thresholds for seed-set, seed growth, phenology, and other processes affecting yield be developed and parameterized from elevated temperature experiments whether field or controlled-environment chambers. In this paper, we describe the status of crop models for dry bean (*Phaseolus vulgaris* L.), peanut (*Arachis hypogaea* L.), soybean (*Glycine max* L.), chickpea (*Cicer arietinum* L.), sorghum (*Sorghum bicolor* (L.) Moench), and millet (*Pennisetum glaucum* L. (R.) Br) in the Decision Support System for Agrotechnology Transfer (DSSAT) for response to elevated temperature by comparison to observed data, and we review where changes have been made or where needed changes remain. Temperature functions for phenology and photosynthesis of the CROPGRO-Dry Bean model were modified in 2006 for DSSAT V4.5, based on observed growth and yield of Montcalm cultivar grown in sunlit, controlled-environment chambers. Temperature functions for soybean and peanut models were evaluated against growth and yield data in the same chambers and found to adequately predict growth and yield, thus have not been modified since 1998 release of V3.5. The temperature functions for the chickpea model were substantially modified for many processes, and are updated for V4.6. The millet model was re-coded and modified for its temperature sensitivities, with a new function to allow the 8–10 day period prior to anthesis to affect grain set, as parameterized from field observations. For the sorghum model, the temperature effect on grain growth rate was modified to improve yield and grain size response to elevated temperature by comparison to data in controlled-environment chambers. For reliable assessments of climate change impact, it is critically important to gather additional temperature response data and to update parameterization and code of all crop models including DSSAT.

1. Introduction

Crop growth models are increasingly being used to assess crop yield impact from future climate change, including increases in both CO_2 and temperature (Rosenzweig et al., 2014). Global atmospheric air temperature and atmospheric CO_2 concentrations ($[CO_2]$) are expected to rise significantly by 2050 and beyond (IPCC, 2015). The $[CO_2]$ is projected to increase to 540 ppm by 2050 under the radiative concentration pathway (RCP) 8.5 scenario or by 2100 under RCP 4.5 scenario, respectively (Van Vuuren et al., 2011). Water deficits are also anticipated to increase, but there is greater uncertainty in rainfall expected for different regions and time periods. The effects of rising CO_2 are overall beneficial and are relatively well understood and well documented as illustrated in several metadata reviews (Amthor, 2001; Ainsworth et al., 2002; Ainsworth and Long, 2005; Kimball et al., 2002). On the other hand, the effects of elevated temperature on crop growth and yield are less well understood, and to the extent of available literature and data, are mostly detrimental, thus reducing yield (Baker and Allen, 1993; Prasad et al., 2002, 2003, 2006a, 2006b; Boote et al., 2005). Elevated temperature effects are also less well modeled although progress is being made by some crop modeling groups (Asseng et al., 2014).

Strong interest and funding of applications of crop models to address climate change impacts have pressed the models into service,

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despite not being adequately updated with recent data on crop response to climate change factors, especially elevated temperature (Boote et al., 2011a). Beyond the immediate need for climate impact assessments, there have been insufficient resources and attention focused on testing and improving the crop models against available data on elevated temperature effects (Boote et al., 2011a, 2011b). Thus, the objective of this paper is to illustrate the status of several of the crop models in the Decision Support System for Agrotechnology Transfer (DSSAT) for their response to elevated temperature by comparison to observed responses under elevated temperature, and to illustrate where changes have been made in the past or where needed changes remain.

The DSSAT software (Jones et al., 2003) contains a suite of crop models patterned after two primary types of models: the CERES family of models (Ritchie et al., 1998) which are RUE-based and simpler, and the CROPGRO family of models (Boote et al., 1998a, 1998b) which are more mechanistic and have more species and genetic coefficients. The CERES family of models has temperature effects on leaf appearance rate, reproductive progress, radiation use efficiency (RUE), and rate of grain-filling (RGFIL). The CROPGRO model has temperature effects on a greater number of processes, because it is based on leaf-level photosynthesis scaled up to hedgerow canopy assimilation (Boote and Pickering, 1994) and it has maintenance respiration and has more mechanistic addition of reproductive sites and seed growth. The CROPGRO model uses a single source code for all its crops, and follows a template approach in which there is a "read-in" species file per crop which contains the parameter relationships for temperature effects on these many processes (Boote et al., 1998a, 1998b). Those external read-in parameterizations take a variety of shapes ranging from 4- or 5-point look up functions, with linear, quadratic, or parabolic interpolations between cardinal temperatures. CROPGRO's temperature relationships affect leaf photosynthesis, maintenance respiration, leaf appearance rate, leaf area expansion, internode (height) expansion, root depth progression, nodule growth rate, N_2-fixation rate, vegetative N re-mobilization, progress toward anthesis/seed-set, progress after seed-set to maturity (latter using a different function), rate of pod addition, and rate of seed growth rate (Boote et al., 1998a, 1998b). Parameterization of some of these functions is based on reliable experiments conducted under temperature-controlled environments, while other temperature functions were solved from field data corresponding to diverse temperature environments (Piper et al., 1998; Sexton et al., 1998; Boote et al., 2002, 2012). It is these functions that will be described in this paper relative to available data on response of several crops to temperature.

A brief summary of general temperature effects on crop growth and yield follows. As temperature increases, crops generally progress more rapidly to anthesis and maturity, and have a shorter life cycle, thus having less time for resource capture, less time for leaf area development, and a shorter grain-filling period and lower yield. This generalization applies only at moderately cool temperatures up until the optimum temperature is reached at which development rate is most rapid. Above that optimum, development rate of many crop species actually plateau at that optimum temperature (do not progress more rapidly), and some actually slow down at supra-optimum temperature. Surprisingly, because of a lack of elevated temperature data, some existing models (including CERES-Maize and CERES-derived maize models, K. J. Boote, unpublished data) incorrectly model the phenology response to supra-optimum temperature by not accounting for this upper plateau or the slow-down phase, and this tends toward too much shortening of the grain-filling phase and too much reduction in yield at elevated temperature, although this may (likely) be compensated in the models by other parameterization. Photosynthesis, despite being a favorite target of plant physiologists, is actually more tolerant of elevated temperature than is reproductive growth which will be highlighted later in this paper. Photosynthesis rate typically increases as temperature increases, then peaks at an optimum temperature followed by a reduction in rate at supra-optimum temperature (however, often the elevated temperature effects that reduce photosynthesis are temporary, with recovery when temperatures recede). Maintenance respiration increases almost exponentially (with Q10 somewhat less than 2) with rising temperature (McCree, 1974), but it is too often incorrectly given as a primary causal factor for reduced yield at elevated temperature. The two most critical two temperature functions that affect grain yield are those affecting the setting of seed (pollen viability/fertility) and individual seed/grain growth rate (Boote et al., 2005). The elevated temperature effect via pollen viability acts during the 8–10 days prior to anthesis and on the day of anthesis (Prasad et al., 2001), which poses two problems for crop models: 1) modelers need to program a window for remembering temperature effects during the 8–10 day period prior to flower opening, and 2) more robust simulations may be attained by modeling age-dependent cohorts of flowers which reach anthesis and form fertilized ovules over a 3–4 week period for indeterminate legumes and over a week or longer for so-called determinate cereals (rice, sorghum, maize) that exhibit a time-spread over which flowers reach anthesis and pollen is shed. There are considerable differences among species in the temperature threshold effects on pollen viability which we will illustrate in this paper. But once successful fertilization occurs, the ovules and growing seed are relatively tolerant of elevated temperature. In addition, seed/grain growth rate is sensitive to temperature, being reduced in rate at elevated temperatures above relatively modest optimum temperatures (such as 24 °C or less for soybean). The growth duration of seeds is longer at cool temperature and shortened at elevated temperature, but only up to a point of the optimum temperature.

The objective of this paper is to illustrate functions affecting sensitivity of phenology, seed-set, seed-growth, and yield to elevated temperature for six DSSAT crop models: peanut, soybean, dry bean, chickpea, sorghum, and millet, by comparison to elevated temperature data used for parameterizing these functions. This paper focuses only on the DSSAT crop models for these six crops, present in the latest DSSAT V4.6.10 release (Hoogenboom et al., 2015). The selection of only these six crops is based on: 1) the availability of elevated temperature response data on four of the crops, and 2) recent code updates of the chickpea and millet models conducted in collaborative projects with ICRISAT scientists (Singh et al., 2014a, 2017).

2. Methods and materials

Data for model evaluation and parameterization came from elevated temperature experiments in sunlight-controlled environment chambers on four of the crops plus field trials on chickpea and millet in India. Elevated temperature experiments were conducted in 2 by 1 m sunlit, controlled-environment chambers at the University of Florida/USDA-ARS-Gainesville on peanut (Prasad et al., 2003), soybean (Pan, 1996; Thomas et al., 2010; Boote et al., 2005), dry bean (Prasad et al., 2002), and sorghum (Prasad et al., 2006a). Those experiments were conducted for season-long growth under temperature-controlled conditions of 32/22, 36/26, 40/30, and 44/34 °C (max/min diurnal cycles) for peanut, soybean, and sorghum, and at 28/18, 31/21, 34/24, 37/27, and 40/30 °C (max/min diurnal cycles) for dry bean. The aerial chamber was 1.5 m tall, and the chamber base was 0.60 m deep, filled with Kendrick fine sand topsoil. Plants were well fertilized and irrigated, and rhizobium was applied to the legumes. The CO_2 concentration was carefully controlled at either 350 or 700 $\pm$ 2 ppm, thus also allowing response to CO_2 to be evaluated (but CO_2 effects will not be discussed here). The diurnal hourly temperature programmed for those chambers is based on Tmax and Tmin followed the Parton and Logan (1981) temperature function, with a sinusoidal shape from sunrise to sunset, followed by an exponential decay function at night to Tmin at sunrise the next day. Dewpoint temperature was maintained 5 °C below the target day and night temperatures. The germination-emergence phase of approximately 8 days was conducted under a common moderate temperature, prior to implementing the temperature treatments. The system used

natural diurnal solar irradiance cycles and natural daylength cycles (generally fairly short days). Solar radiation for purposes of modeling was assumed to be the same as the external solar radiation, as the clear 'Sixlight' plastic (Taiyo Kogyo Co., Tokyo) had 88% transmission, but there is considerable back-scatter off the back panels such that internal radiation basically was assumed the same as external radiation as observed by Kim et al. (2004) for similar sunlit, controlled-environment chambers. Chamber side walls were shaded with black plastic shade cloths to mimic a closed canopy. The crop canopy remained intact and undisturbed until harvest which allowed reliable large land-area sampling of biomass, grain yield, harvest index, seed number, and seed size at maturity. For details on experimental methods and environmental control, see the respective research papers (Prasad et al., 2002, 2003, 2006a).

For DSSAT model simulations, the soil, weather (temperature, CO_2, solar radiation), and management conditions (sowing date, plant population, row spacing, etc.) were entered into the respective files needed for running the models. For the CROPGRO-style crops, the model simulates the same hourly diurnal temperature pattern as described above based on Parton and Logan (1981). Model simulated outputs were compared to observed final biomass, pod yield, grain yield, grain number, grain size, and harvest index. For some of the crops, external "read-in" species files were modified to change parameterization of temperature functions for processes affecting phenological progress, photosynthesis, pod-set (seed-set), and seed-growth rate. In those cases, figures were designed to illustrate model simulations based on default versus modified parameters.

3. Results and discussion

3.1. Dry bean

The CROPGRO-Dry Bean model in DSSAT was modified by K. Boote in May 2005 (personal communication) and the species changes were included in DSSAT V4.0 of August 31, 2005, based on data for dry bean (*Phaseolus vulgaris* L.) cv. Montcalm reported by Prasad et al. (2002). Details of that experiment can be found in Prasad et al. (2002); however, only data from the elevated CO_2 treatment at 700 ppm are shown here for two reasons: the temperature response was continuous (five levels) for the high CO_2 treatment, and source (CO_2 supply) limitations on assimilation were presumed less likely to affect temperature responses. We first looked at crop phenology predictions. Observed time to anthesis was considerably delayed above 34/24 °C temperature, but the default model did not predict that (Fig. 1). The default phenology temperature function was good below 26 °C, but progress to anthesis was too rapid at temperatures above 26 °C mean (corresponding to the 31/21 °C diurnal cycle treatment). Therefore modifications of species parameterization for phenology were made. The temperature parameter Topt2 for progress to anthesis, was decreased from 37 to 31 °C, while the Tfail (failure temperature to zero relative rate) was reduced from 45 to 44 °C. These two parameter changes provided the correct simulation of the temperature-induced delay of the time to anthesis (Sim – Modified line in Fig. 1), at least up to 32 °C (we decided to be conservative in fully modifying the function from 32 to 35 °C). The time from anthesis to maturity was predicted to be too short, but this was addressed by increasing the genetic coefficient SDPM, the phase duration from beginning seed to physiological maturity, with no change in the temperature function affecting the rate of progress after beginning seed. The default photothermal coefficients were modified from default Andean-type RedKloud cultivar values (FLSH from 3 to 4 pd, and SDPM from 18.4 to 25 pd) as we lacked coefficients for Montcalm. With the modification of the temperature functions for phenology, the RMSE for prediction of first flower was reduced from 6.54 to 3.16 d, and the D-index (Willmott, 1981) was increased from 0.45 to 0.87. With the new temperature function and the adjusted phase durations, the prediction of physiological maturity was improved with lower RMSE (1.50 d) and higher D-index (0.99), but improvement was mostly related to adjusting FLSH and SD-PM. At 35 °C mean (40/30 °C), there were no mature pods (only many small green parthenocarpic pods with no seeds), thus maturity was not reached, and was not definable (data point on graph only shows the date of sampling final plant biomass and parthenocarpic pods).

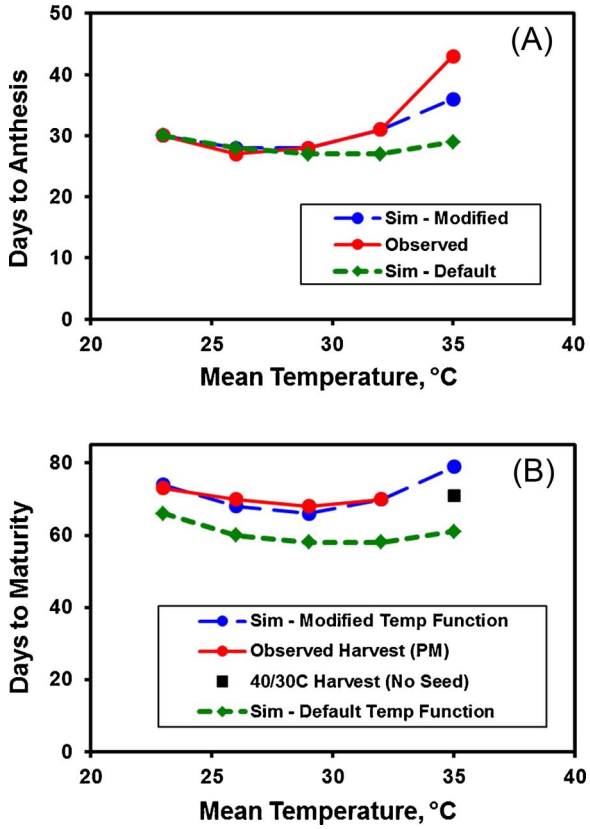

Fig. 1. A) Days to anthesis and B) days to maturity for dry bean Montcalm as affected by temperature with new function compared to default temperature function. Temperature function for reproductive progress prior to seed set was changed as follows: Topt2 from 37 to 31 °C, Tmax from 45 to 44 °C. FLSH was increased from 3 to 4 physiological days (pd) and SDPM was lengthened from 18.4 to 25 pd. Sim – Modified is an improvement.

Next, with modified phenology temperature functions and updated life cycle, we evaluated the prediction of biomass-related measurements of total aboveground mass (Fig. 2A), total pod mass (Fig. 2B), and total seed mass (Fig. 2C). The model was run with N balance off, because the crop was well-fertilized and N was not limiting in the study. With updated phenology and the default photosynthesis temperature function, the model under-predicted crop biomass, especially at the highest temperatures. In fact, predicted biomass was near zero at 35 °C. The pod and seed mass predictions generally followed the same trend of under-prediction as temperature increased. Improved predictions of total biomass and pod yield were obtained by making the light-saturated leaf photosynthesis rate (actually electron transport) less sensitive to temperatures above 30 °C. The Topt2, the point of 0.8 relative rate for this look-up function, was increased from 31 to 34 °C, and the Tfailure point was increased from 36 to 42 °C. These changes in sensitivity of leaf photosynthesis were sufficient to improve predictions of biomass (RMSE decreased from 1559 to 553 kg ha^{-1}, and D-index increased from 0.83 to 0.96) and pod yield (RMSE decreased from 547 to 246 kg ha^{-1} and D-index increased from 0.97 to 0.99). For seed yield, there was no improvement although D-index remained high at 0.98. Seed size response to temperature, with minor adjustment of potential size from 660 to 610 mg per seed, was accurately predicted with either version, with low RMSE (0.114 and 0.115) and high D-index (0.92 and 0.92) (Fig. 3A). Therefore, there was no need for modifying the single

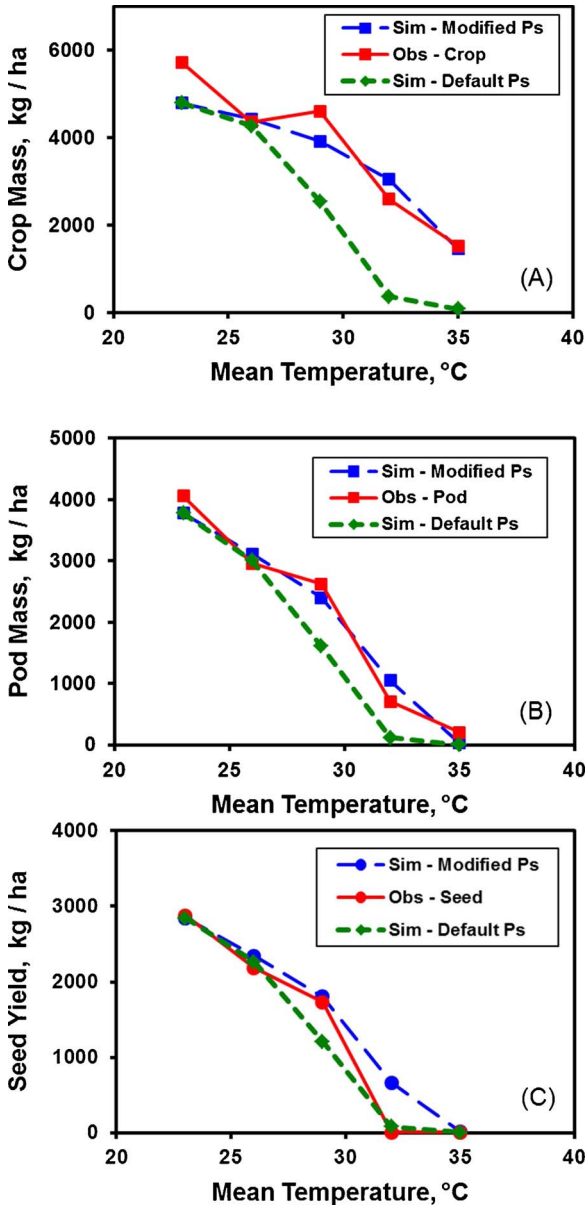

Fig. 2. A) Total crop mass, B) pod mass, and C) seed yield at harvest of dry bean Montcalm as a function of temperature. All simulations used the modified temperature function for reproductive phenology and adjusted SDPM. The simulations compare the newly-modified function against the default temperature function for photosynthesis.

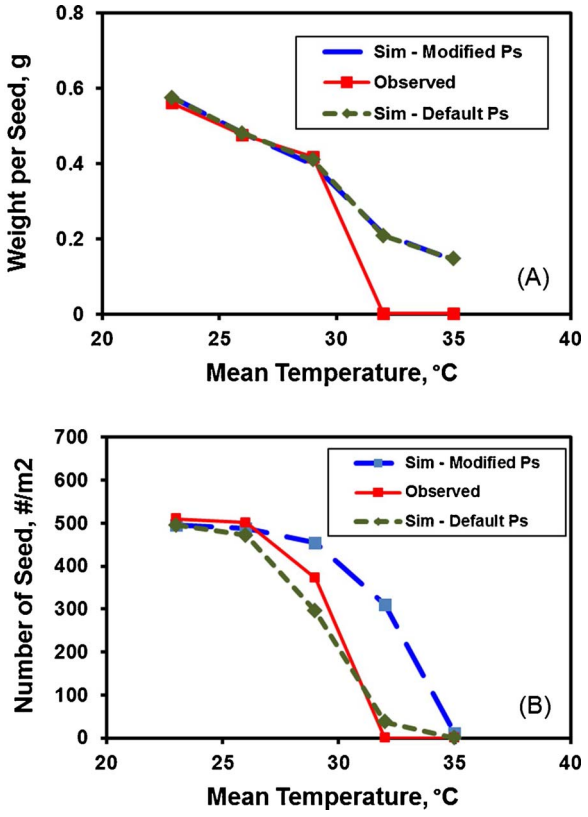

Fig. 3. A) Weight per seed, and B) seed number per m2 of dry bean Montcalm grown as a function of temperature. All simulations used the modified temperature function for reproductive phenology and adjusted SDPM. The simulations compare the newly-modified function against the default temperature function for photosynthesis.

seed growth rate temperature function. However, there is a "future" need to create a somewhat cooler upper cut-off (Tfail) temperature that prevents seed/pod set (Fig. 3B), as the model allowed a few seeds to set at 32 °C (37/27 °C) when, in reality, none were set (final seed number versus temperature had a relatively high RMSE of 144 number m^{-2} although D-index was good at 0.98). Improved predictions of seed yield and seed number were potentially achievable by decreasing the Tfail (cutoff) for podset by 1 or 2 °C. However, that modification was not adopted because we desired to be conservative in model modification from prior versions based on only a single data set. One of the complications is that many small pods (and podwall mass) were added in the real crop at 32 °C, but seed were aborted, as shown by observed values at 32 °C in Figs. 2 B, C, and 3 B. On the other hand, the daily pod and seed cohort system in CROPGRO is programmed to successfully carry "permanently" a pod at the moment when seed are added in that cohort. In summary, the temperature functions for pod-set and single seed-growth rate were acceptable (and not changed), but the temperature functions for leaf photosynthesis and the rate of progress to anthesis/beginning seed were modified. With these changes, the seed yield, pod yield, total biomass, and seed size response to temperature had the correct declining shape with rising temperature (Figs. 2 and 3). These modifications improve on the temperature functions programmed by the original developers of the dry bean model (Hoogenboom et al., 1994). These changes have been in the Dry Bean model released as V4.0 since August 31, 2005.

3.2. Peanut

The CROPGRO-Peanut model in DSSAT is a case where no model modifications were found necessary after evaluating against data on peanut (*Arachis hypogaea* L.) cv Georgia Green grown under different temperature treatments and 350 ppm CO_2 in the sunlit, controlled environment experiments of Prasad et al. (2003). Simulations with the default model are compared to observed temperature response for total biomass and pod mass in Fig. 4. While the model defaults were deemed sufficient, there were suggestions of directions of change that may be needed in the future. The shape of total biomass at maturity is quite comparable to that observed at the higher three temperatures, so we concluded that temperature parameters for leaf photosynthesis did not require modification. Although simulated absolute biomass is somewhat higher than observed, caution for over-calibration is warranted because of questions of solar irradiance received inside the chambers. The simulated pod yield response in Fig. 4 is close to observed, but suggests that the model is too sensitive in reducing yield at the two highest temperatures. The seed number versus temperature (Fig. 5A), weight per seed versus temperature (Fig. 5B), and the seed harvest index versus temperature (Fig. 5C) suggest that the upper failure temperatures for pod-set and for seed growth rate need to be pushed up

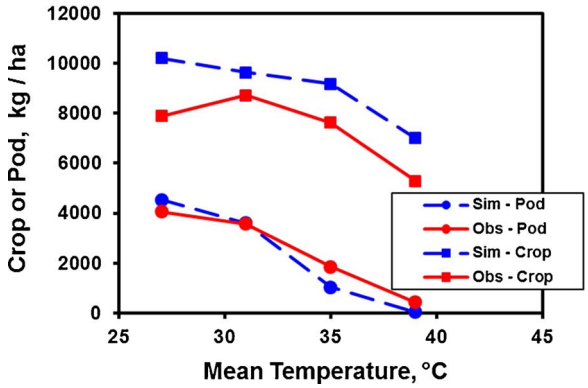

Fig. 4. Simulated and observed total crop mass and pod mass at harvest of peanut Georgia Green as a function of temperature and grown at 350 ppm CO_2. All simulations used the default temperature functions for CROPGRO-Peanut model. Redrawn from Fig. 4 of Boote et al. (2011a).

higher, although additional observations are needed to confirm the response before making these modifications. Improved predictions were potentially obtained for pod yield, seed harvest index, seed number and seed size if the upper failure point for podset was moved up from 40 to 44 °C and that for single seed growth rate was moved up from 41 to 45 °C (those results not shown here, and not used in the present model). We do not trust the observed seed size response as much because the soil temperature was allowed to float with air temperature control and would have been lower than air temperature. It is important to note that none of these proposed changes have been made to the CROPGRO-Peanut model. While correct temperature parameterization is important for those conducting climate change impact assessments, this test is against just a single experiment, with no confirmation from another source. Upon confirmation with additional experiments, we will be inclined to make further changes. An interesting contrast of species is that the upper failure temperature for zero peanut yield occurs at 40 °C, by contrast to dry bean which had total failure at 32 °C. Peanut is much more heat tolerant.

3.3. Soybean

The CROPGRO-Soybean model in DSSAT is another case where no model modifications were found necessary after evaluating against data on Bragg (*Glycine max* (L.) Merr.) soybean grown in the sunlit, controlled environment experiments (Pan, 1996; Thomas et al., 2010; Boote et al., 2005). Model simulations are compared to observed response to temperature for reproductive phenology, including time from sowing to anthesis (R1) and physiological maturity (R7) in Fig. 6A, and time from anthesis to physiological maturity (R1-R7) in Fig. 6B. The model defaults were deemed sufficient for predicting seed yield and seed harvest HI (Fig. 7A and B), but there were suggestions of directions of change in temperature functions affecting phenology that may be needed in the future. For example, the time from sowing to anthesis (under short daylength of the 11 February sowing) was most rapid at 31 °C mean temperature, with slight delay at higher or lower temperature. The default parameterization showed too much delay in time to flower with temperature above 30 °C, which was improved by modifying the four-point linear temperature function from 6, 26, 30, 45C, to 6, 28, 32, 55 °C. Rate of progress from anthesis to beginning seed was slowed as temperature increased above 23 °C and thus caused later physiological maturity (Fig. 6A). Based on the observed data, the optimum temperature for most rapid progress from anthesis to maturity was a surprisingly 23 °C (Fig. 6A), which also coincided with 23 °C being the optimum for the most rapid seed growth rate and final size of seed (Thomas et al., 2010). The default simulations in Fig. 6B included the effects of post-anthesis daylength effects with CSDL (Critical Short Day Length) of 12.33 h and R1PRO of 0.504 h (hours decrease in CSDL

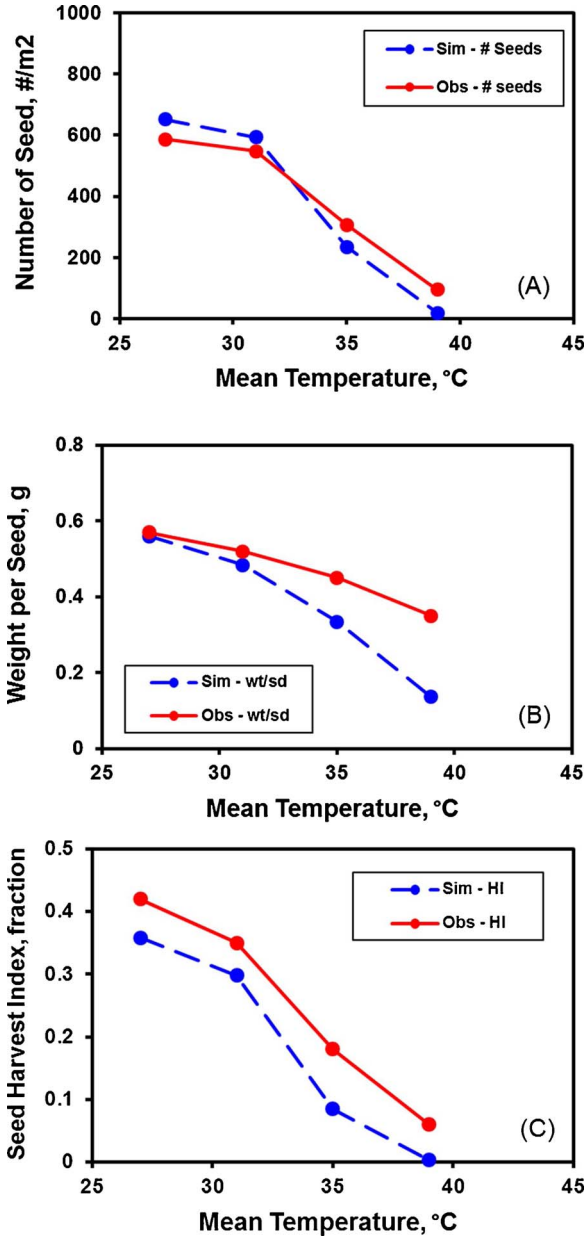

Fig. 5. A) Seed number per m2, B) weight per seed, and C) seed harvest index at harvest of Georgia Green peanut as a function of temperature and grown at 350 ppm CO_2. Simulations used default temperature functions for CROPGRO-Peanut model.

for post-anthesis development), which caused later simulated maturity and longer R1-R7 than observed (reproductive growth occurred during April and May in Florida during which daylength was increasingly longer than 12 h). For this exercise, the direct modification was to remove the daylength effect by setting CSLD to 13.0 h and setting R1PRO to 0.001; but that simulation had the wrong shape for temperature effect during post-anthesis (see Fig. 6B, with the original temperature function). As a result, the temperature function (Tb, Topt1, Topt2, Tfail) for post-anthesis development was modified from −15, 26, 34, 45 °C, to −15, 18, 26, 60 °C. The −15 °C for Tb was discovered nearly 20 years ago, based on solving post-seed-set duration against field data (Grimm et al., 1994). The reproductive phase from beginning seed to physiological maturity as well as the computed effective seed filling duration (based on harvesting tagged pods) were slightly increased going from the coolest to warmest temperature treatments (Thomas et al., 2010), thus most of the elevated temperature effect on phenology was the delay from anthesis until rapid seed growth commenced,

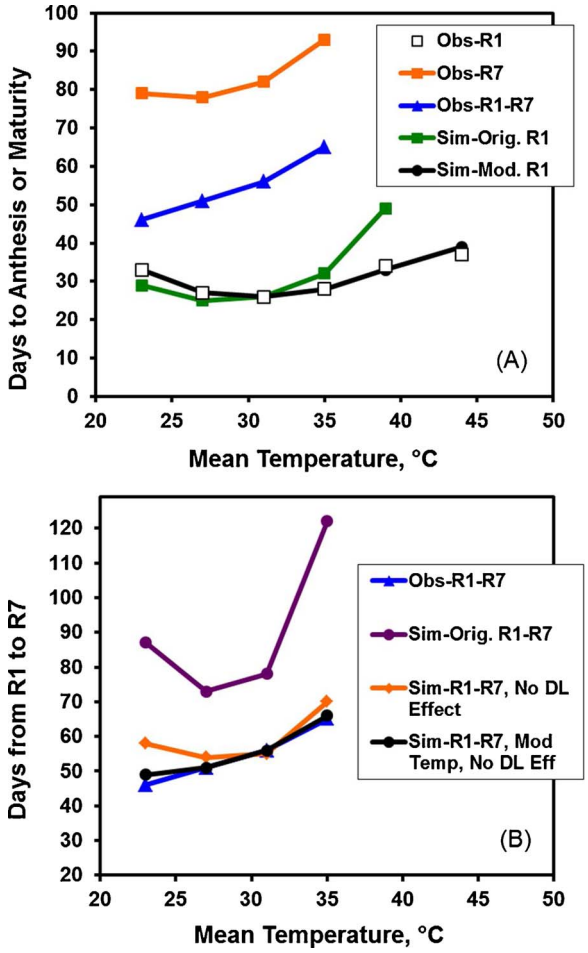

Fig. 6. A) Observed days from sowing to anthesis (R1), sowing to physiological maturity (R7), anthesis to physiological maturity (R1-R7), and simulated days from sowing to anthesis (default and modified) for Bragg soybean in response to temperature. The four-point temperature function was modified from 6, 26, 30, 45 °C, to 6, 28, 32, 55 °C. B) days from anthesis to maturity (R1-R7), observed and simulated with three cases (1.) Default. (2.) Removing daylength effect, and (3.) Modifying temperature function and removing daylength effect on post-anthesis. For case 3, the four-point temperature function for anthesis was modified from 6, 26, 30, 45 °C, to 6, 28, 32, 55 °C, and that for post-anthesis, from −15, 26, 34, 45 °C, to −15, 18, 26, 60 °C.

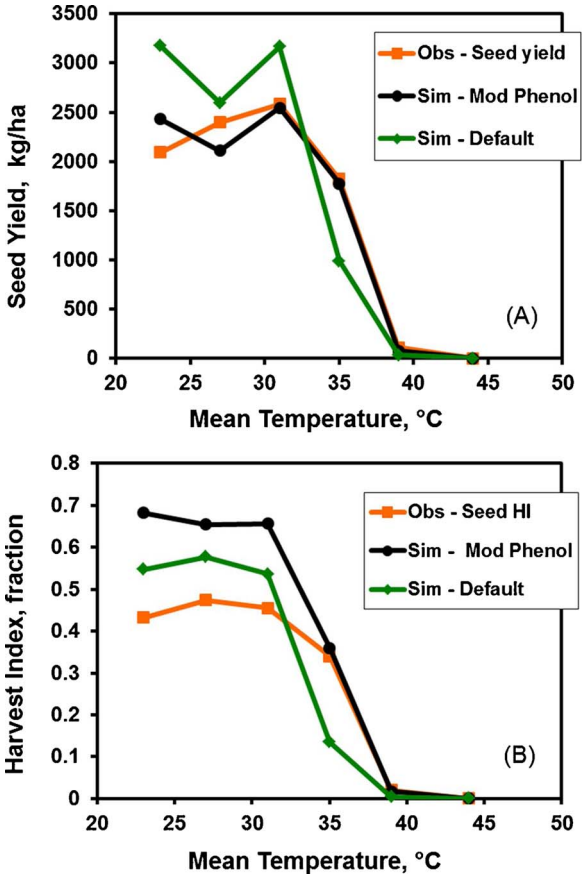

Fig. 7. A) Seed yield response to temperature for Bragg soybean, showing observed values, simulated with default model, and simulated with model modified for temperature and daylength functions on phenology only. B) Seed harvest index response to temperature for Bragg soybean, showing observed values, simulated with default model, and simulated with model modified for temperature and daylength functions on phenology only. Fig. 7A redrawn from Fig. 5 of Boote et al. (2011a).

although single seed growth rate was reduced as temperature increased (Thomas et al., 2010). We have confirmed this phenomenon of elevated temperature-induced delay from anthesis to onset of rapid seed growth, smaller seed size, as well as the somewhat longer time from beginning seed to physiological maturity in recent experiments on MG 3 soybean Maverick (Boote et al., unpublished data), so we conclude this is likely a general phenomenon for soybean.

Fig. 7 illustrates observed yield response to temperature compared to simulations with the default and modified model (modified for the phenology as described above). No other model changes were made. Both the default and the modified model versions substantially captured the reduction in seed yield (Fig. 7A) and seed harvest index (Fig. 7B) as temperature exceeded 30 °C mean temperature, being progressively reduced until temperature reached 39–40 °C (This is nearly identical to the failure temperature for peanut). It is important to point out that this yield response to temperature for both soybean and peanut is caused primarily by the functions affecting rate of pod addition (pollination and seed-set) and the rate of individual seed growth. Those functions were taken from data on individual seed growth rate measured under different temperatures by Egli and Wardlaw (1980). Recent work by Thomas et al. (2010) is in agreement with the function and data of Egli and Wardlaw. Those functions have been used in the soybean model for the past 30 years (Wilkerson et al., 1983; Boote et al., 1998b), and are sufficiently good that they do not warrant changing. It is the pre-anthesis as well as post-anthesis temperature functions (anthesis to onset of rapid seed growth) that should be modified. Fig. 7B shows that seed harvest index is likely the most valuable single characteristic for screening cultivars for heat tolerance, as it shows the same sharp decline as yield does above 30 °C, approaching failure to zero HI at 39–40 °C. The relatively high simulated HI at cooler temperatures and the subtle differences in simulated HI between the default versus modified model are caused by the minor phenology changes that were made. While the absolute HI at cooler temperatures should be somewhat discounted, we are confident that the elevated temperature effects on yield and HI above 30 °C are caused by reduced seed-set and reduced single-seed growth rate.

3.4. Chickpea (Cicer arietinum L.)

The CROPGRO-Chickpea model was adapted more than 20 years ago by Singh and Virmani (1994). The model has not been widely used until recently, when the CG system (IFPRI and ICRISAT) became interested in using the chickpea model to hypothesize genetic improvement (virtual cultivars) for improved yields, especially under climate change. As part of this exercise, we decided that we had to improve the parameterization of the chickpea model for response to climate change factors, especially temperature, as the template for model adaptation in the first instance had been CROPGRO-Peanut which is a warm-season legume quite different from chickpea. Therefore, major changes were

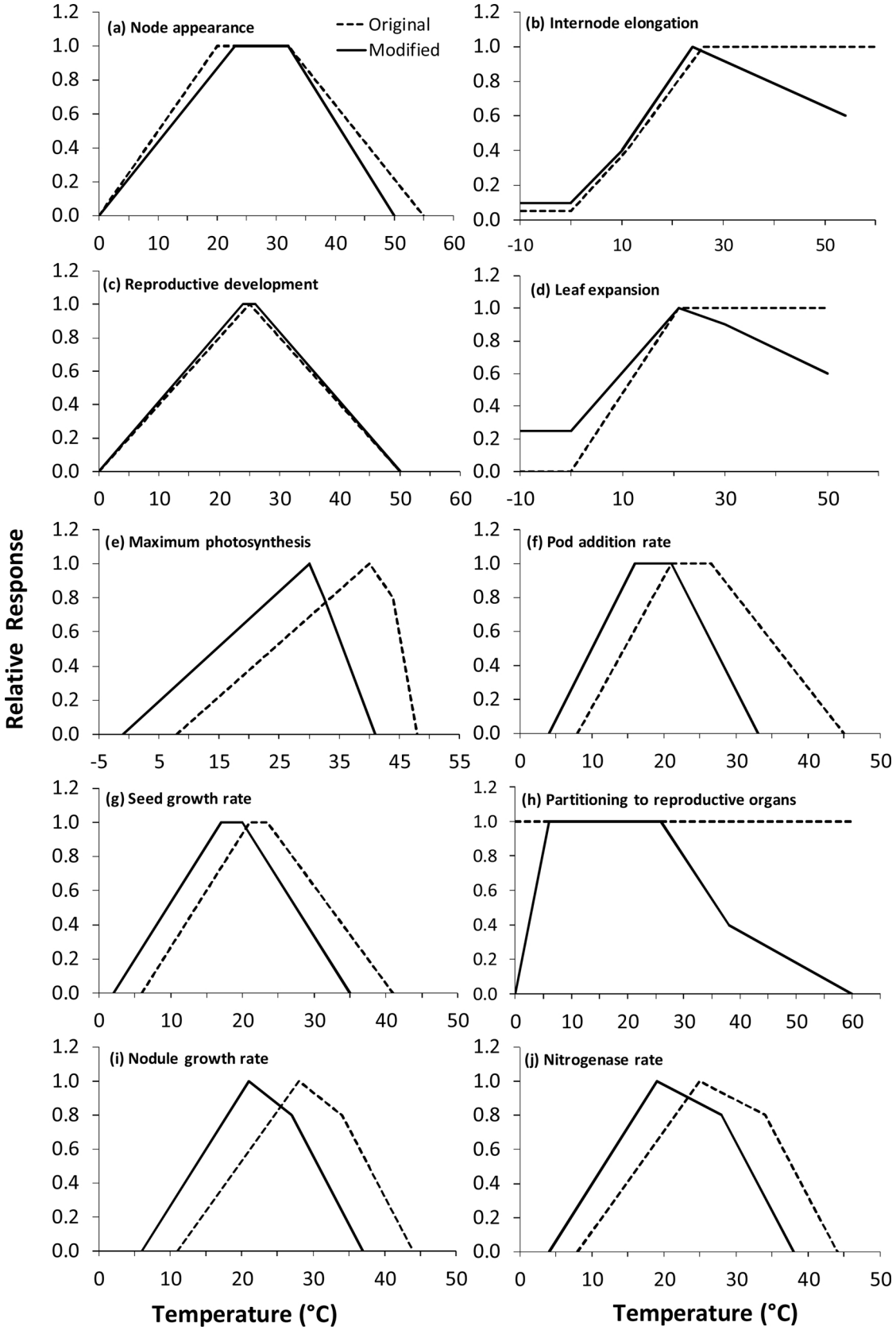

Fig. 8. Original (dashed line) and modified (solid line) response functions to temperature for (a) node appearance, (b) internode elongation, (c) reproductive development, (d) leaf expansion, (e) maximum leaf photosynthesis rate, (f) pod addition rate, (g) seed growth rate, (h) partitioning to reproductive organs, (i) nodule growth rate, and (j) nitrogenase rate for the CROPGRO-Chickpea model (Figure reprinted from Singh et al., 2014a). Figure 1 from Singh et al. European Journal of Agronomy 52:123-137.

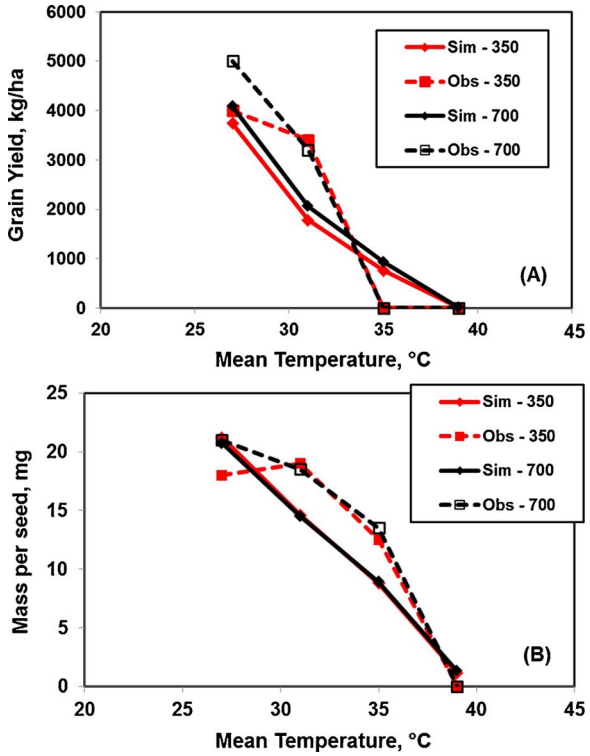

Fig. 9. A) Simulated grain yield and (B) mass per seed at harvest compared with observed data of sorghum grown in two atmospheric CO_2 concentrations (350 and 700 ppm) and different mean air temperatures. Observed data obtained from controlled environment studies of Prasad et al. (2006a). Sim, Simulated; Obs, Observed. Redrawn from Fig. 1 of Singh et al. (2014b).

made to many of the temperature-related parameterizations of the CROPGRO-Chickpea model (Singh et al., 2014a) on processes of photosynthesis, nodule growth rate, nitrogenase activity, pod addition rate, seed growth rate, and temperature limits on partitioning to seed. ICRISAT scientists provided extensive growth and yield data on chickpea for multiple sites that were used to re-parameterize and re-calibrate the model. In addition, the effects of supra-optimal temperature on pod-set and single seed growth rate were parameterized from elevated temperature experiments of Wang et al. (2006), all the while being sure that the new parameterization worked for the extensive field experimental data. Fig. 8 (from Figure 1 of Singh et al., 2014a) illustrates how the temperature parameterizations were modified from the old default (created in 1994) compared to the new values for V4.6 (modifications were made on DSSAT V4.5 prior to May 2013. These were probably in a re-release of V4.5 in 2013 or 2014). It is obvious that the initial parameterizations from the 1994 paper were not particularly thorough, as the cardinal temperatures for many processes had to be modified considerably. The temperature functions for leaf appearance rate, rate of reproductive progression, temperature limit to reproductive partitioning, leaf expansion, and internode elongation were relatively unchanged. But the temperature functions for leaf photosynthesis, pod addition rate, seed growth rate, nodule growth rate, and nitrogenase rate were modified considerably, with generally lower Tb and lower Topt1 but greater sensitivity to elevated temperature for most of the processes in Fig. 8. In defense of the initial model developers, the model now uses only leaf-level photosynthesis, but the default old version of the model had used the daily canopy version (C-version), which could have been calibrated to give the correct biomass growth response to temperature for the few data sets used in initial model creation. A corollary message can be taken from Fig. 8, as it illustrates the type of 4- or 5-point functions used in the DSSAT models to parameterize the 0–1 (relative) temperature sensitivity where one must also define the potential rate of a process at the optimum temperature. There are other function shapes available that use quadratic (parabolic) response between cardinal temperatures (the parabolic shape is used for DSSAT's peanut and soybean models for their pod addition and single seed growth rate functions).

As part of the ICRISAT "virtual cultivar" project, we tried to mimic the possibility suggested by data of Devasirvatham et al. (2012a, 2012b) that there may be a potential 3 °C shift in temperature sensitivity between heat-sensitive versus heat-tolerant chickpea genotypes. In order to mimic heat-tolerance, the two right-side parameters (Topt2 and Tfail) for both pod addition rate and seed growth rate were moved 3 °C higher with the caveat that the susceptible genotype should show some limitation in hot field environments and the tolerant genotype would be able to set more seeds (and maybe larger seeds). This was guided in part by the elevated temperature experiments of Wang et al. (2006).

3.5. Sorghum

The other two crops discussed in this paper are the CERES-based sorghum and millet models. Both use RUE approach for growth and do not simulate explicitly simulate photosynthesis or respiration, and have fewer temperature-dependent processes as well as fewer cultivar parameters. Similar to the chickpea case, there was interest from the CG system (IFPRI and ICRISAT), to use the DSSAT sorghum model to hypothesize genetic improvement (virtual cultivars) for improved yields, especially under climate change. As part of this exercise, we first evaluated the sorghum model against elevated temperature data on grain yield, grain number, and grain size of sorghum [*Sorghum bicolor* (L.) Moench] cv. DeKalb 28E grown in the sunlit, controlled environment experiments of Prasad et al. (2006a). The sorghum model, in contrast to CROPGRO, lacks temperature effect on grain-set, and only allows temperature effects on RUE, grain growth rate (RGFIL), and phenology. The paper by Singh et al. (2014b) describes modification of the temperature effects on the single grain growth rate (RGFIL) which reproduced reasonably well the effect on grain yield (Fig. 9A) and grain size (Fig. 9B). The two upper temperature thresholds for RGFIL values (Topt2, and Tfail) were changed from 48, 50 °C to 27, 35 °C mean daily temperature, based visually on the cardinal temperatures from Prasad et al. (2006a), although the model was not explicitly calibrated to that data. The upper threshold temperatures on RGFIL had clearly been ignored by prior CERES-Sorghum model developers. The new function helped to reproduce the decline in yield from optimum to zero as temperature increased from 26 to 35 °C mean temperature (observed yield was nil at mean of 35 °C). Much of that effect was from the RGFIL which reduced grain growth rate, resulting in the reduction of grain size (Fig. 9B). The simulated effect on grain number (Fig. 10) was less successful in being modified for the correct reason, as the simulated

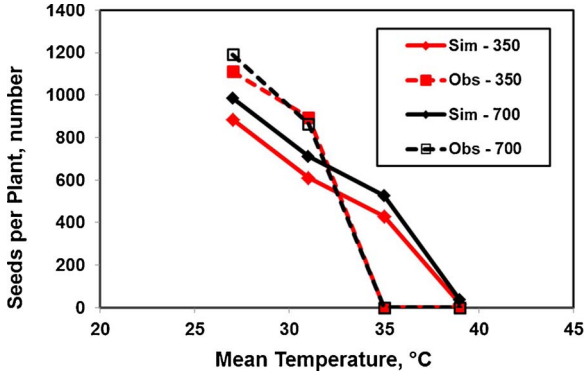

Fig. 10. Simulated seed number per plant at harvest compared with observed data of sorghum grown in two atmospheric CO_2 concentrations (350 and 700 ppm) and different mean air temperatures. Observed data obtained from controlled environment studies of Prasad et al. (2006a). Sim, Simulated; Obs, Observed.

reduction in grain number at elevated temperature also results from temperature effects in the model that reduce LAI at supra-optimal temperature. In reality, elevated temperature did not reduce LAI in the experiment, so the model in its present form may be giving the right yield reduction for the wrong reason. The code for simulating LAI response to temperature needs to be further investigated, and the model needs to include new coding and functions that allow seed-set to be modified by elevated temperature. The CERES-Sorghum model is presently being re-programed by Myriam Adam (personal communication, 2016) with advice from DSSAT modelers, and those features will be re-evaluated, including the functions for temperature effect on grain-set and grain growth rate.

It should be emphasized that pollen viability and pollen numbers are primary reasons for failure of grain-set and grain yield in sorghum at elevated temperature, so it will be very important to bring in temperature effects on pollen viability as they are known to affect grain number set in rice (Matsui et al., 1997) dry bean (Prasad et al., 2002, peanut (Prasad et al., 2003) and sorghum (Prasad et al., 2006a). The time period for affecting pollen viability and grain-set is likely to be the 8–10 day period prior to anthesis as reported for other crops (Prasad et al., 2001), and that creates the need to model temperature effects based on temperature during the 8–10 day window prior, and including anthesis. There is likely also a short window of time after anthesis during which ovules abort because of limited carrying capacity (daily assimilate supply relative to total number of grains growing), but that is not necessarily related to pollen viability issues associated with rising temperature.

An added note of importance and interest is that sorghum is surprisingly just as sensitive to elevated temperature as rice, with both rice and sorghum having zero yield and yield failure at 40/30 °C (Tmax/Tmin diurnal temperature cycles) (Baker et al., 1992a,1992b; Baker and Allen, 1993; Boote et al., 2005; Prasad et al., 2006a). By way of comparison, peanut and soybean produce yield at 40/30 °C, and only fall to zero yield at about 44/34 °C; thus those two legumes are 4–5 °C more tolerant than rice and sorghum. Another interesting feature of the sorghum crop was that considerable delay in anthesis was observed under elevated temperature with time to panicle emergence being increased from 41 days after sowing (DAS) at 32/22 °C and 40 DAS at 36/26 °C to 60 days at 40/30 °C temperature where only 10% panicle emergence occurred. No panicles emerged at 44/34 °C. Anthesis occurred 3–4 days after panicle emergence in all treatments. We think that sorghum's reported heat-tolerance is mostly actually related to delay in anthesis and grain growth until a cooler time of year, because plants exposed to elevated temperature and then removed from the chambers to ambient outdoor temperatures had head exertion about a month later, albeit with mostly damaged panicles and poor grain-set.

3.6. Pearl millet (*Pennisetum glaucum L. (R.)*)

As for the chickpea and sorghum cases, there was interest from the CG system (IFPRI and ICRISAT) to use the DSSAT CERES-Millet model to hypothesize genetic improvement (virtual cultivars) for improved yields, especially under climate change. While we lacked data from controlled-environment temperature studies, the ICRISAT scientists provided a valuable data set (Fig. 11) on seed-set of pearl millet cultivars grown in the hottest state of India (Gupta et al., 2015). These results were used to add code and parameterize a new function called RGSET into the CERES-Millet model. Similar to the sorghum model, the default millet model had previously lacked a temperature effect on grain-set, and only allowed temperature effects on RUE, grain growth rate (RGFIL), and phenology. In this case, we made many additional code changes to the CERES-Millet model (Boote, personal communication, 2015; Singh et al., 2017) for processes of tillering, leaf area growth, grain-set, and single grain growth rate. Also, model re-calibrations were made against the extensive data provided by ICRISAT (165 total treatment combinations over multiple sites, N fertilization,

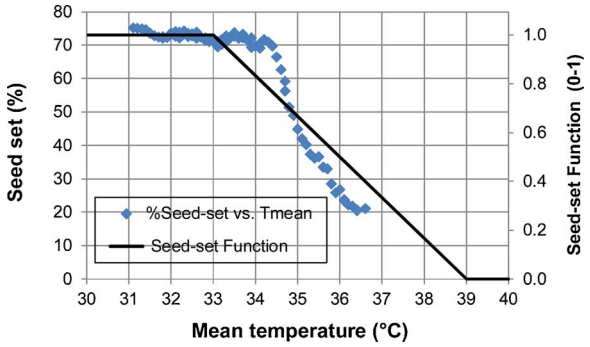

Fig. 11. Percent seed set of millet versus mean air temperature for millet grown in field trials conducted during March to May in India (Figure re-drawn from data of Gupta et al., 2015 and used for creating the CERES-Millet model RGSET function for temperature effect on setting seed (solid line describes the present seed-set function in the model)).

row spacing, plant population, and water limitation). New temperature functions were added for leaf area growth (RGLAI) where prior coefficients were pulled out of the code and placed in the species file, as also done for grain-set (RGSET). The shape of former existing temperature functions on RUE (PRFTC) and grain growth rate (RGFIL) were modified. Table 1 lists the Tb, Topt1, Topt2, and Tfail for the RGSET and RGFIL functions as modified. The Tb, Topt1, Topt2, and Tfail for the RUE (PRFTC) and RGLAI were adjusted to 11, 22, 35, 48 °C and 8, 23, 32, 42 °C, respectively. Of particular note, the new grain-set function (RGSET) was based on the percent grain-set versus mean temperature (Fig. 11) in the study reported by Gupta et al. (2015). The Topt2 for relative grain-set of 1.0 was parameterized to 33 °C (threshold), and complete failure of grain-set (to 0.0) was parameterized to 39 °C mean temperature (see solid line in Fig. 11). Pearl millet appears to have heat tolerance similar to that of peanut and soybean. For comparative purposes, the threshold of 33 °C mean daily temperature corresponds to a daily Tmax of 41 °C.

3.7. Heat-tolerant cultivars within a species

It is important that temperature thresholds for grain-set and grain growth rate be set accurately before conducting climate impact assessment, and especially if heat-tolerant cultivars are considered as one option for adapting to climate change for target regions (Gourdji et al., 2013; Teixeira et al., 2013). This particular exercise was attempted by ICRISAT scientists relative to peanut, sorghum, chickpea, and pearl millet as part of a Global Futures project funded by Gates, via IFPRI, to ICRISAT and other CG centers. Singh et al. (2013) created heat tolerant cultivars of peanut by pushing up the Topt2 and Tfail temperatures by 2 °C for pod addition and for seed growth rate, as well as upper limit on

Table 1
Cardinal Topt2 (upper optimum) and Tfailure temperatures (◦C) for seed-set and individual seed growth rate (GR) used in six DSSAT crop models. Shapes are parabolic on hourly temperatures for legumes and linear lookups on daily mean for the cereals. CERES-Maize is like CERES-Sorghum.

Function	Peanut[a]	Soybean[a]	Drybean[b]	Chickpea[c]	Sorghum[c]	Millet[d]
Seed-set – Topt2	26.5	26.5	25.0	21.0	–	33.0
Seed-set – Tfail	40.0	40.0	36.0	33.0	–	39.0
Seed GR – Topt2	23.5	23.5	25.0	20.0	27.0	27.0
Seed GR – Tfail	41.0	41.0	38.0	35.0	35.0	60.0

[a] Set in V3.5 (1998).
[b] Set in V4.5 (2006).
[c] Set in V4.6 (2014).
[d] Set in V4.7 (2017).

partitioning to reproductive. For Anantapur, India site, heat tolerant cultivars increased yield 1–3% under present climate and 5–9% under future climate. For Sadore, Niger site, heat tolerance increased yield 2–3% under current climate and 9–12% under future climate. Their future climate for 2050 followed the UKMO-HADCM3 GCM model with SRES A1B scenario. Singh et al. (2014a) followed the same approach with chickpea evaluated for 4 sites in India and 4 sites in East Africa, also using the same future climate scenario. They created heat tolerant cultivars by pushing up the Topt2 and Tfail temperatures and partitioning limit temperatures (see Fig. 8f–h) by 3 °C. For those regions in India and East Africa, the heat tolerant cultivar trait for chickpea increased yield from 0 to 9%, but often gave insignificant increases, being much less important than drought tolerance. The same methods were applied with the CERES-Sorghum model for India and West African sites (Singh et al., 2014b). In this case, only the Topt2 and Tfail of RGFIL was available, and the two thresholds were pushed up by 2 °C, Topt2 from 27 to 29 °C, and Tfail from 35 to 37 °C. The benefit to sorghum yield was site-specific, being 0–4% and 8–12% for current and future climate, respectively, for Akola, India, whereas the effect at Indore, India was less than 3% even under future climate. For two sites in West Africa, the benefit to yield was 0–3% for current climate and 5–9% under future climate. Similar analyses of heat tolerance traits of pearl millet were conducted by Singh et al. (2017). The heat-tolerant trait involved increasing the Topt2 and Tfail for RGFIL and RGSET by 2 °C. The trait benefit to yield was highly site-dependent, giving no increase in yield for 2 cool sites in India under current and future climate, but giving 3–12% yield increase at 4 other sites under current climate and 6–17% increase under future climate. For two West African sites, the yield increase from heat tolerance was 2–5% under current climate and 6–13% under future climate. Boote et al. (2011a) reviewed literature for heat tolerance of soybean cultivars and concluded that only a small degree of heat tolerance (2–3 °C) was available from the germplasm evaluated. He conducted simulations of creating more heat-tolerant soybean cultivars, pushing up the Topt2 and Tfail for grain-set and grain-growth rate by 2 °C. This heat tolerance trait increased yield by 1.6% under current Florida climate and 3.4% under 2 °C warmer future climate in Florida. Benefits were almost nil for upper Midwestern USA (Iowa) even under 2 °C warmer climate.

3.8. Future improvements, research needs, species comparison for heat-tolerance

Prior to conducting climate change impact assessments or simulating effects of climate change on heat-tolerant cultivars, it is important that upper thresholds for seed-set and seed growth rate be developed and parameterized from elevated temperature experiments (whether field or sunlit controlled-environment chambers). Field environments varying from cool to naturally occurring elevated temperatures are difficult to set up in an orthogonal way that maintains similar daylength, radiation, and soil conditions, thus full characterization requires use of controlled-environment studies or heat tents in the field. The T-FACE experiments are a good attempt to increase temperature of crops under field conditions, but the temperature increment possible is small and does not allow defining the full range of elevated temperature effects. Each of these methods has unique problems. We believe that the sunlit, controlled-environment chambers used in Florida and elsewhere (Fleisher et al., 2011) are probably more reliable than growth chambers that have low light intensity and high humidity, because temperature damage effects on grain yield are stronger at low radiation levels and are enhanced with high humidity systems in which foliage and pod temperatures are warmer than under low humidity environments.

For the purpose of comparing species for heat-tolerance, Table 1 illustrates the upper threshold temperature dependences (Topt2 (the highest optimum temperature) and Tfailure) of these six DSSAT crop models. Chickpea, being a cool-season legume, has the lowest Topt2 and Tfail for seed-set and single seed growth rate compared to the other crops. Dry bean is not a winter-season crop, but it is grown in cool environments and its Topt2 and Tfail are slightly higher than those of chickpea. Peanut and soybean, being warm-season crops have higher Tfail values that are about 4 °C higher than those for dry bean. These four CROPGRO crops use hourly temperature in their functions. The two CERES modeled crops, sorghum and millet, use mean daily temperature in their functions which creates a somewhat different meaning for the threshold. Sorghum in the experiments was more sensitive to elevated temperature than soybean or peanut, as sorghum had an upper failure temperature 4 °C cooler (at 35 °C mean, contrasted to 39 °C mean where soybean and peanut fail in grain yield). The CERES-Sorghum model also has the disadvantage of setting temperature sensitivity of yield using only rate of grain growth (RGFIL), with one function creating much of the effect, even if simulated final yield is correct for the wrong reason. CERES-Maize, while not evaluated here, similarly lacks temperature effect on grain-set, and its RGFIL was re-parameterized in about 2014 for V4.6 (also in a late V4.5 release), to be exactly the same as the RGFIL of CERES-Sorghum. Elevated temperature data for grain-set of maize is sparse, and in absence of data, we assumed that maize heat tolerance is similar to rice and sorghum. A new function was added to the CERES-Pearl Millet model to allow temperature effect on grain-set (grain numbers) associated with temperature during the 8–10 day phase prior to rapid grain growth (during the short phenological phase prior to grain-set). Grain-set of millet was parameterized against mean daily temperature based on observations under very hot field condition experiments conducted by ICRISAT scientists. The grain growth rate function of millet was less confidently parameterized.

4. Conclusions: model modifications for six contrasting species

In summary, this paper has documented the status of elevated temperature sensitivities of parameterization that affect grain yield of six DSSAT crop models. It described how various functions were parameterized, the data on which the functions were based, and the present status of the crop models. Temperature functions for two of the DSSAT models (soybean and peanut) have not been modified since 1998 (Boote et al., 1998a, 1998b) and have been shown to work well by comparison to data collected from sunlit, controlled-environment chambers. Temperature functions for photosynthesis of the CROPGRO-Dry Bean model were modified based on observed growth and yield of Montcalm cultivar grown in the same system. The changes to dry bean were substantial and have been in the DSSAT since 2006. For CROPGRO-Chickpea, very major changes were made for temperature parameterization of many processes (photosynthesis, nodule growth, nitrogenase activity, pod-set, seed-growth rate) as described in Singh et al. (2014a). These changes are now in the DSSAT V4.6 release. The CERES-Sorghum model, having few options for temperature sensitivity, was modified for its temperature sensitivity of single-seed growth rate (RGFIL), and these changes are described in Singh et al. (2014b). These parameter changes for sorghum are in DSSAT V4.6 (and possibly in a late release of V4.5 of the software). The CERES-Millet model modifications are described in a paper by Singh et al. (2017) and will be in the next release of DSSAT (V4.7).

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